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A note on the significance of sugar in the tubers of Solanum tuberosum

O. Butler

(WITH PLATE 2)

Sugar accumulates in the tubers of the potato during the rest period when they are subjected to low temperatures, and, at least this is the general opinion, at the time of germination. In other words sugar develops at a time when the various vitalistic phenomena are inactive and again when the life processes are proceeding actively.

I

During the rest period two factors influence the accumulation of sugar in the tubers of the potato: temperature and oxygen supply. Both these factors may act independently of one another or additively. I shall, however, for convenience, consider them separately.

TEMPERATURE

The effect of temperature on the accumulation of sugar in potato tubers was studied years ago by Müller-Thurgau* and, as the results he obtained have not been disproved, I will simply briefly review them, adding some data of my own in confirmation.

The belief is very tenaciously rooted in the popular mind that a potato becomes sweet only when it is frozen. A frozen potato never becomes sweet, moreover a potato does not freeze at 0° C., whence probably the origin of this notion. Potatoes, in fact, may be stored at 0° C. for a period of time without being injured, Müller-Thurgau having kept them at this temperature in some of his experiments for as long as one hundred days.

Taking 0° C., then, as the lowest temperature at which potatoes may be safely stored, Müller-Thurgau found that when the rates of sugar accumulation at 0° C., 3° C., and 6° C. were compared the following relation was approximately obtained, x being the amount of sugar formed at 0° C.

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* Müller-Thurgau, H. Ueber Zuckeranhäufung in Pflanzentheilen in Folge niederer Temperatur. Landw. Jahrb. **11**: 757–828. 1882.

$$\frac{x}{3.6} \text{ at } 3^\circ \text{ C. and } \frac{x}{7} \text{ at } 6^\circ \text{ C.}$$

He also observed that individual potatoes of the same variety showed marked variations in the rapidity with which sugar accumulated in their tissues, but that if at 0° C. sugar accumulated in relatively small amount in the tubers of a given variety, then no accumulation would occur at 6° C., and conversely, if sugar was formed rapidly at 0° C., then a temperature of 8° C. would be usually necessary to effect the same result. At 10° C. sugar never accumulated.

The fact brought to light by Müller-Thurgau that different varieties of potatoes exhibit differences in the rapidity of sugar accumulation is readily confirmed, as the following table shows.

TABLE I

SUGAR ACCUMULATION IN DIFFERENT VARIETIES OF POTATOES STORED AT 1°–5° C. FOR 28 DAYS

	Percentage reducing sugar in potatoes*		
Variety of potato	At beginning of experiment	After 28 days	Daily increase
Triumph	0.59	0.97	+0.013
American Wonder	0.88	0.85	−0.001
Rural New Yorker	0.17	1.01	+0.03
Early Ohio	0.15	1.25	+0.039
Early Rose	0.42	0.86	+0.015
Red Alcohol	0.10	1.42	+0.047
Rusty Rose	0.43	1.10	+0.023
Blue Victor	0.53	1.22	+0.024
McCormick	0.43	1.04	+0.021

Müller-Thurgau found, taking his results for 3° C., as these more nearly approach the average temperature at which the potatoes were stored in the above experiment, that the daily increase during a period of 30 days was 0.021 per cent, results which are of the same order as those given in the above table.

According to Müller-Thurgau sugar does not accumulate in resting potatoes when they are stored at a temperature of 8° C.

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* All the quantitative determinations given in this paper were kindly made for me by Mr. F. B. Morrison, Madison, Wis.

It would also appear as if potatoes stored at 8°–10° C. not only do not accumulate sugar but do not reconvert it into starch as occurs at higher temperatures (this is Müller-Thurgau's view of the matter), or dispose of it through respiratory activity. The amount of sugar present in the potatoes when they are placed in storage at this temperature suffers little change. This fact is clearly shown in the following table:

TABLE II

CHANGES IN SUGAR CONTENT OF DIFFERENT VARIETIES OF POTATOES AFTER STORAGE AT 8°–11° C. FOR 34 DAYS

	Percentage reducing sugar in potatoes		
Variety of potato	At beginning of experiment	At end of 34 days	Increase
Triumph	0.59	0.43	−0.16
American Wonder	0.88	0.65	−0.23
Rural New Yorker	0.17	0.24	+0.07
Early Ohio	0.15	0.16	+0.01
Early Rose	0.42	0.31	−0.11
Red Alcohol	0.10	0.17	+0.07
Rusty Rose	0.43	0.38	−0.05
Blue Victor	0.53	0.45	−0.08
McCormick	0.43	0.39	−0.04

When potatoes containing sugar are stored at 20° C. the sugar gradually disappears due to increased respiration and reconversion to starch (Müller-Thurgau). However, if the potatoes remain sufficiently long at 20° C. for germination to be initiated, an increase in the sugar content is liable to take place. The aberrant results in the following table may be accounted for on these grounds.

TABLE III

LOSS OF SUGAR IN POTATOES STORED AT 20° C. FOR 21 DAYS

	Percentage reducing sugar in potatoes		
Variety of potato	At beginning of experiment	At end of 21 days	Decrease
Triumph	0.59	0.22	−0.37
American Wonder	0.88	0.05	−0.83
Rural New Yorker	0.17	trace	−0.17
Early Ohio	0.15	0.08	−0.07
Early Rose	0.42	0.13	−0.29
Red Alcohol	0.10	0.15	+0.05
Rusty Rose	0.43	0.37	−0.06
Blue Victor	0.53	0.40	−0.13
McCormick	0.43	0.65	+0.22

When potatoes containing sugar are placed at 20° C. respiration immediately increases to a very marked extent, while in the case of similar potatoes containing none or only traces of sugar the increase is very slight. The respiration of the potatoes containing sugar, while very rapid at first, reaches a maximum in one and a half or two days, and then gradually decreases until it becomes equal to that of potatoes containing little or no sugar.

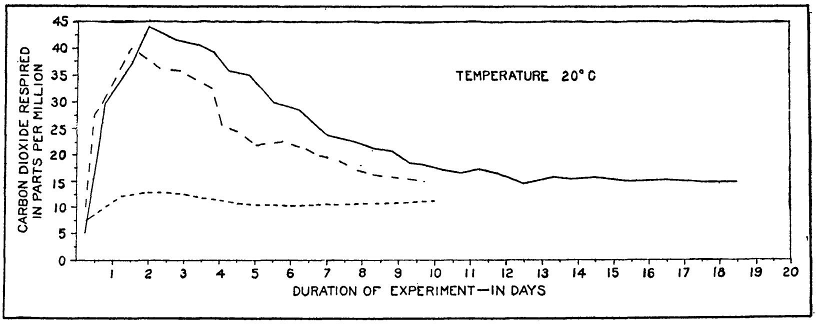

FIG. 1. (After Müller-Thurgau.) Respiration of potatoes containing different amounts of sugar at 20° C. Legend:

——— Respiration of 50 potatoes containing an average of 1.7814 per cent reducing sugar.

– – – – Respiration of 50 potatoes containing an average of 1.464 per cent reducing sugar.

- - - - - - Respiration of 50 potatoes containing none or only traces of reducing sugar.

The results obtained by Müller-Thurgau are very striking and are well illustrated in the above graph taken from his work. (FIG. 1.)

It is perfectly obvious that the respiratory activity of potatoes is more influenced by the presence of sugar than by temperature. Sugar is essentially a limiting factor. This is well illustrated in the second graph (FIG. 2), in which the respiratory activity of

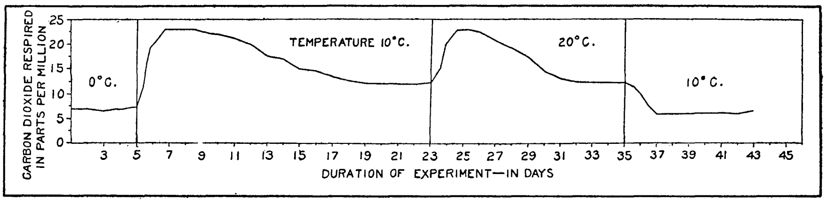

FIG. 2. (After Müller-Thurgau.) Influence of change of temperature on respiratory activity of potatoes initially rich in reducing sugar.

potatoes stored at 0° C., then at 10° C., then at 20° C., and again at 10° C., is compared. It will be seen at once that when potatoes were placed at 10° C. respiration immediately increased, then fell gradually until the potatoes were placed at 20° C., when it rose again to the same maximum as before but decreased more rapidly and, after being placed at 10° C. again for a short while, became almost equal to what it had been when the potatoes were stored at 0° C. It should be noted that the experiments just recorded were begun after the potatoes had been kept for 28 days at 0° C., i.e., the potatoes used were rich in sugar.

Müller-Thurgau believed that when potatoes containing sugar were placed at 20° C. the sugar that disappeared was partly used up in respiration, and partly reconverted to starch, as the disappearance of the sugar could not be all accounted for by the amount of carbon dioxide exhaled. In performing his experiments Müller-Thurgau sliced his potatoes longitudinally, using one half for immediate analysis and the other for analysis at the end of the experiments. Under these conditions, even when the proper corrections for loss of weight due to evaporation are made, some of the sugar will undoubtedly go to the formation of the suber produced along the cut surface, and not unlikely, the increase in the percentage of starch obtained was due to the hydration of the cellulose that had been recently or was being laid down. The question, however, is deserving of further study.

OXYGEN

We have seen that during the rest period sugar may be made to accumulate in potatoes by storing the tubers at temperatures varying between 0° C. and 6° C., but that at 8°–10° C. the amount of sugar (when any was present) remained stationary. The relation of the oxygen supply to the accumulation of sugar in potatoes therefore may be studied conveniently at 8°–10° C. In the experiment which I have performed on this subject I used the Sir Walter Raleigh variety of potato and the tubers were placed in tubulated bell jars of the usual pattern:

Bell jar no. 1 contained 1,934 grams of potatoes, and the tubules were stopped with cotton, thus allowing a free diffusion of air.

Bell jar no. 2 contained 1,936 grams of potatoes and was connected with a water siphon by means of which approximately 8 per cent of the volume of the contained air was renewed daily.

Bell jar no. 3 contained 1,897 grams of potatoes and was connected with a water siphon by means of which approximately 0.8 per cent of the volume of the contained air was renewed daily.

Within a few days the air in all the bell jars became saturated with water vapor. The experiment was discontinued after 90 days, when the potatoes in the different bell jars were analyzed and found to contain sugar as follows:

Bell jar no. 1, 0.09 per cent sugar; bell jar no. 2, 0.22 per cent sugar; bell jar no. 3, 0.66 per cent sugar. The effect of reducing the oxygen supply on the accumulation of sugar in potatoes is, therefore, quite marked, though not nearly so notable as that of low temperature.

II

The view is very generally held that sugar accumulates in potatoes at the time of germination and that this accumulation is essential thereto. According to de Vries* sugar begins to appear in potatoes just prior to germination but before the buds show any signs of growth. Resting potatoes, he says, contain for the most part no sugar, its appearance indicating the initial stages of germination. The sugar first appears in the neighborhood of the eyes, more precisely in the parenchymatous tissue surrounding the bundles leading to them. At first present in small amounts, it soon increases in quantity, developing in all parts of the tubers. During their early period of growth the shoots contain starch but no sugar, though the tubers themselves are full of the latter, the larger amount being in the medulla, the smaller in the cortex. When the shoots are 8 mm. long sugar is found in them only in isolated spots, but somewhat later it is generally distributed, and this condition remains unchanged until they come through the soil.

The accumulation of sugar in potatoes has not, however, as regards germination, any particular physiological significance. As in the case of resting potatoes the amount of sugar found in germinating tubers is greatly influenced by the milieu in which germination takes place. Potatoes germinating at a relatively low temperature contain more sugar than potatoes germinating at relatively high temperatures, and potatoes germinating in soil contain more sugar than those germinating in a cellar. Again, the distribution of sugar in potatoes germinating in a cellar, for instance, is irregular. All these facts clearly indicate that the metabolism of germination is not concerned primarily in the distribution or degree of accumulation of sugar.* I will give a few examples in illustration.

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* Vries, H. de. Keimungsgeschichte der Kartoffelknollen. Landw. Jahrb. 7: 236. 1878.

Conditions favorable for germination are not necessarily favorable for the accumulation of sugar. For instance, on the 26th of April, 1912, I examined a number of Early Ohio potatoes, and they contained as a rule no sugar (PLATE 2, FIG. 6) though the sprouts were replete with it. A sample of these potatoes was placed in the ice compartment of an ice chest for 20 days, after which the potatoes composing it contained sugar as indicated in FIG. 2, 5. At the same time similar potatoes from the cellar contained sugar as indicated in FIG. 1 and 4. It is worthy of note that the potatoes stored in the ice chamber (FIG. 2, 5) resembled very closely the potatoes shown in FIG. 7, as regards distribution of the accumulated sugar. The distribution of sugar illustrated by FIG. 7 was rather common in stored potatoes during March, 1911, which stored potatoes had been at no time subjected to a temperature below 6° C. It is therefore clear that the low temperature had not induced irregularities in metabolism.

A glance at the plate will also force upon one the conclusion that the degree of germination has no effect upon the distribution of sugar. Neither is there any connection between presence or absence of sugar in the cortex with corresponding changes in the medulla. The medulla may contain sugar even in large amounts and the cortex give no reaction for it (FIG. 3, 7); again the cortex may contain sugar and the medulla be free from it (FIG. 1), though such cases appear to be rarer than the former; again the cortex may contain sugar in large amounts near the suber and be almost free from it near the line of the medulla, which in turn may be more or less replete with it. Conditions illustrated in FIG. 2, 5, 9 are also not uncommon.

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*The distribution of sugar in potatoes can be followed by boiling thin slices of the tubers in Fehling's solution for a few minutes, when traces of sugar will be indicated by a yellow coloration and an abundance by a red coloration, various shades of orange indicating intermediate amounts.

The distribution of sugar in germinating potatoes, considered with reference to the budding eyes, is also worthy of note. If one cuts longitudinal slices through potatoes in which the apical buds alone have sprouted he will find almost invariably that there is less sugar in the tubers immediately below the shoots than elsewhere. The conditions illustrated in FIG. 2, 5, 7, in which the medulla colors orange in Fehling's solution except for small areas beneath the insertion of the shoots and around the buds, may be also observed.

Qualitative tests having indicated that in germinating potatoes sugar occurred in less amounts near the apices than toward the bases and having also given indications that the bases were usually richer than the middle portions, I thought it would be well to have these results confirmed by quantitative analyses. The results obtained were as follows.

TABLE IV

DISTRIBUTION OF SUGAR IN GERMINATING POTATOES

Percentage reducing sugar in potatoes				Remarks
Variety	Apical zone	Middle zone	Basal zone	
Early Ohio	0.12	.28	.59	Single tuber.
Early Ohio	None	.15	.42	Composite sample of 10 tubers.
Early Ohio	Trace	.35	.88	Single tuber.
Early Ohio	Trace	.46	.50	Single tuber.
Early Ohio	None	.35	.85	Single tuber.
Early Ohio	0.17	.59	.77	Single tuber.

TABLE IV confirms entirely the conclusions deducible from qualitative tests. Potatoes contain little or no sugar near their apices, sometimes nearly as much in their middle as in their basal portions, and sometimes much more towards the base than in the middle. It may be observed that Müller-Thurgau* found that resting potatoes were richer in sugar at the base than at the apex, and we have seen that this is generally true also of germinating potatoes.

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* *Loc. cit.* p. 763.

The buds in potatoes tend to be more numerous around the apices, and one would expect, therefore, that during the rest period as well as at germination metabolic activity would be greater in the apical portions. One of the consequences of this increased activity in the apices of the resting potatoes would be a lesser accumulation of sugar and the difference in the percentage present, as one proceeded towards the base, would be the more noticeable, the less ready the translocation of the sugar from one part of the tubers to another: from the seats of lesser activity to the seat of greater activity. The data given in TABLE IV as well as the qualitative results illustrated in PLATE 2 show rather definitely, it seems to me, that there is little if any translocation from remote to budding parts even in germinating potatoes. Were the translocation of sugar a normal and necessary function in the metabolism of germination, its distribution would be more regular and constant; one would find a definite relation existing between cause and effect. The distribution of sugar (when present) in germinating and resting potatoes is not essentially different,* and it would seem, therefore, that its appearance in quantity just before or at germination should be ascribed, at least in part, to metabolic changes induced by another agent, or other agencies.

DURHAM, NEW HAMPSHIRE.

Description of plate 2

FIG. 1. Longitudinal section through Early Ohio from cellar, 16th May 1912.

FIG. 2. Longitudinal section through Early Ohio stored in ice chest 20 days, 16th May 1912. Compare with FIG. 1.

FIG. 3. Longitudinal section through Rural New Yorker from cellar, March 1911.

FIG. 4. Longitudinal section through Early Ohio from cellar, 16th May 1912.

FIG. 5. Longitudinal section through Early Ohio stored in ice chest 20 days, 16th May 1912. Compare with FIG. 1.

FIG. 6. Longitudinal section of Early Ohio from cellar, 26th April 1912.

FIG. 7. Longitudinal section of Early Ohio from cellar, 8th March 1911.

FIG. 8. Longitudinal section through Triumph from cellar, March 1911.

FIG. 9. Longitudinal section through Triumph from cellar, March 1911.

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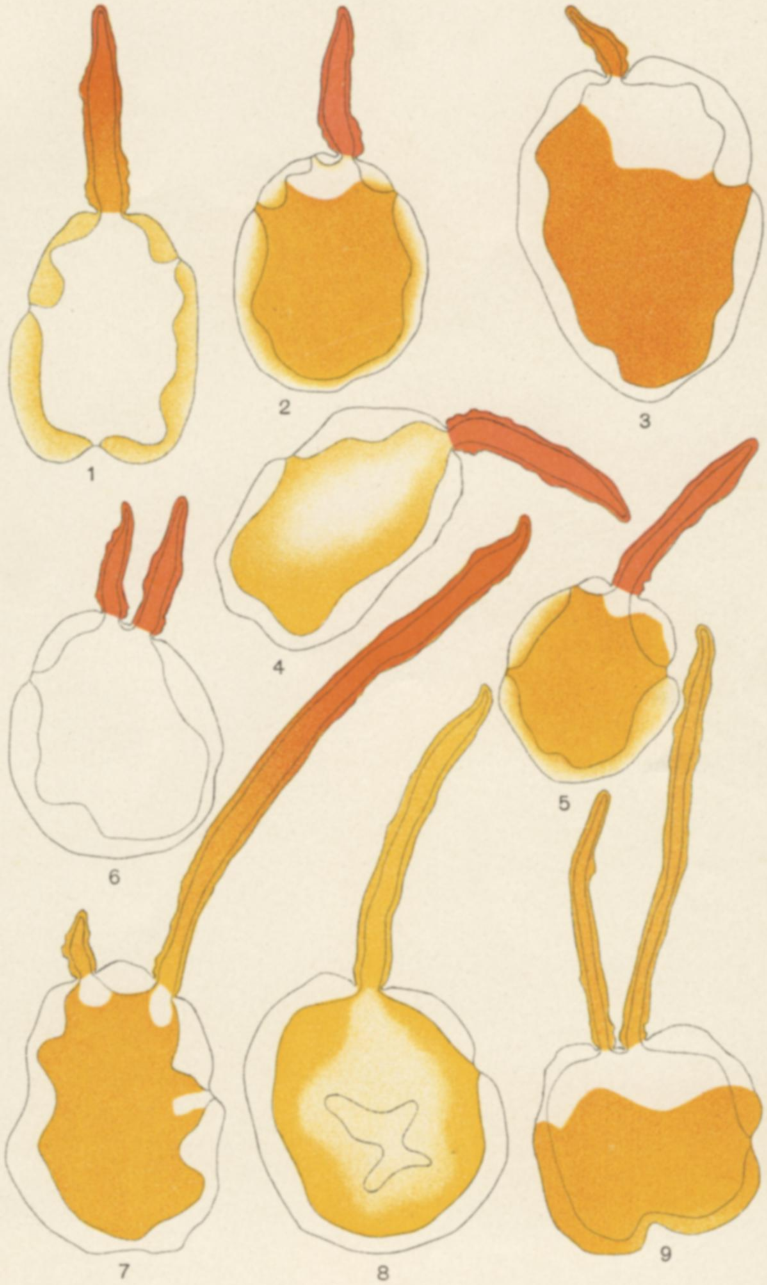
* It is well to point out that germinating potatoes as well as resting potatoes may contain no sugar (cf. FIG. 6).



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BUTLER: SIGNIFICANCE OF SUGAR IN POTATOES